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Evolution of Epiphytism in Ferns and Lycophytes with an Emphasis on Davalliaceae

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This paper reviews studies of the phylogeny and evolution of epiphytism in ferns, with an emphasis on Davalliaceae. The family forms the largest, generally epiphytic monophyletic clade with Polypodiaceae including grammitids. Several other lineages include epiphytes. Molecular phylogenies suggest that the davallioid-polypodioid epiphytes diverged from the secondary hemi-epiphytic Oleandraceae in angiosperm-dominated forests in the Paleogene. The evolution of epiphytism in vittarioids and lycophytic *Huperzia* may be derived directly from terrestrial ancestors. The stepwise evolution of epiphytes is characterized by the ecological shift of gametophytes from the ground to trees following sporophytes, while the abrupt evolution involves the simultaneous shift. Furthermore, reversals from epiphytes to secondary hemi-epiphytes or to terrestrial plants are also likely in other ferns. Precise identification of life forms in the field offers a sound basis of research on epiphyte evolution. There are several morphological traits correlated with life-form change (e.g., rhizome length and dorsiventrality; absorbing or adhering roots; peltate, stalked, dense scales), as well as physiological traits. Epiphytic gametophytes are strap-shaped, ribbon-like or filamentous, branched, gemmiferous and long-lived in, e.g., grammitids, Hymenophyllaceae and vittarioids, while, like terrestrial gametophytes, they are heart-shaped and monocarpic in, e.g., Davalliaceae and Polypodiaceae. Comparative eco-physiological research of gametophytes is needed to investigate the transitions from terrestrial to epiphytic gametophytes. Interactions between epiphytes and hosts should be clarified to understand the evolution of epiphytism. Mildly hemiparasitic epiphytes, e.g., *Pyrrosia piloselloides* (Polypodiaceae), probably obtain water and nutrition from their hosts and may represent a further step in the evolutionary sequence.

Key words: ecological shift, epiphytism, gametophyte, life form, parasite, phylogeny, pteridophyte

Epiphytism is one of the major life forms of plants. Epiphytes account for about 9% of vascular plants and about 25% of ferns and lycophytes (Zotz 2013a). Regionally they account for about 30% of tropical South American vascular plant species (Gentry & Dodson 1987), about 50% of pteridophyte species on Mt. Kinabalu (tropical Asia), about 36% in Mesoamerica, and 49% and 42% in Costa Rica at the Monteverde Forest Reserve and La Selva Biological Station, respectively (Parris *et al.* 1992, Moran *et al.* 2003). In temperate rainforests, in e.g., Chile and New Zealand, epiphytic communities are dominated by

ferns and lycophytes (Zotz 2005). Because of life on trees, epiphytes use limited above-ground water and nutrients, and are diverse in the water economy and patterns of metabolism (Richards 1996). Benzing (1989) recognized holo-epiphytes (obligate epiphytes), facultative epiphytes, and hemi-epiphytes in vascular epiphytes in a broad sense. Among them, hemi-epiphytes are generally primary hemi-epiphytes (e.g., *Ficus*), which grow as epiphytes early in their life history and later become terrestrial by rooting into the soil, while secondary hemi-epiphytes are reversely terrestrial early and become epiphytic toward

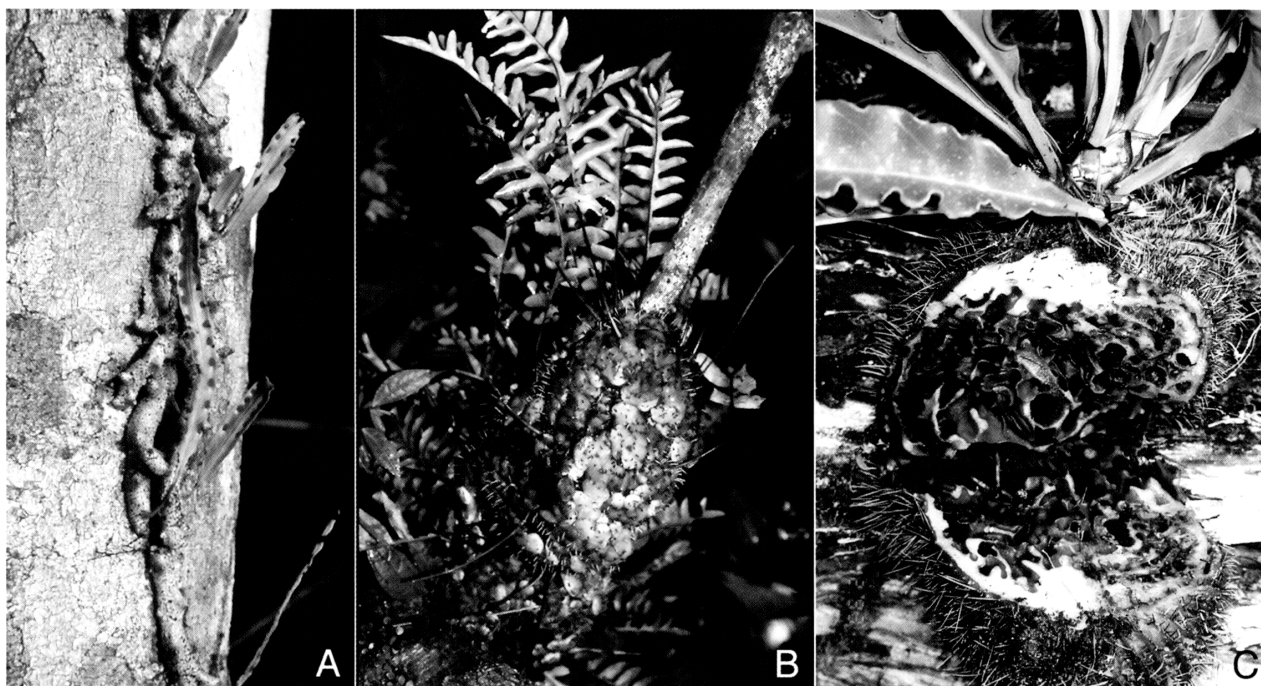


FIG. 1. Myrmecophilous epiphytes. A. *Lecanopteris sinuosa* (Wall. ex Hook.) Copel. (Polypodiaceae) with thick, cylindrical, hollow rhizome (Seram, Indonesia). B. *Lecanopteris carnosa* (Reinw.) Blume with flattened, lobed, hollow rhizome (Kalimantan, Indonesia). C. *Myrmecopodia* (Rubiaceae) with spiny tuberous stem cut obliquely showing ant-nest-like hollows (Papua, Indonesia). Black dots in B and C are ants scampered out from rhizome holes.

maturity (Putz & Holbrook 1986). Hemi-epiphytes are usually secondary in ferns, while they are primary in some species.

Deficiency in water and nutrients is arguably the most important abiotic constraint in the epiphytic habitat (Zotz & Hietz 2001). A species of *Polypodium* (Polypodiaceae) is restricted to host trees (phorophytes or supports) with high water-holding capacity of the tree bark (Callaway *et al.* 2002). Fern epiphytes often grow among bryophytes, which provide soil-holding microhabitats while competing with the ferns. The distribution of epiphytic ferns within the canopy in a Mexican cloud forest is correlated with the relative water content via their physiological traits (Hietz & Briones 1998). Ferns with low tolerance to drought grow on the base of trees or in the shady zone in the canopy, while other ferns in humid cloud forests have xeric adaptations, such as coriaceous leaves, succulent rhizomes, dense leaf scales. A few species growing in exposed locations appear to be poikilohydric or rapidly tolerate high water deficits. Field observations show that epiphytes grow in different habitats with various abiotic conditions (Holtum 1938, Johansson 1974, ter

Steege & Cornelissen 1989, Tsutsumi & Kato 2006, Watkins *et al.* 2006, Watkins & Cardelús 2009). Low-trunk epiphytes prefer relatively high humidity and low light conditions, while high-canopy epiphytes grow in high drought and strong light conditions. In the *Asplenium nidus* L. complex, different types identified by *rbcL* sequences grow at different heights under different light intensities, although these types are closely related to each other (Murakami *et al.* 2000). High-canopy epiphytes (e.g., *Lecanopteris*) are ant plants harboring ants in the rhizome, which symbiotically supply nutrients (Fig. 1). Climbers and secondary hemi-epiphytes are relatively low. Many epiphytes grow on tree trunks or branches, while others, such as vittarioids, grow in the axils of tree branches that are prone to hold soils or humus. Occasionally, plants grow on rocks, indicating that tree bark and rock surfaces are equivalent substrata for epiphytes and lithophytes.

Systematically, epiphytes *sensu lato* are distributed throughout a wide range of pteridophytes (ferns and lycophytes), suggesting recurrent origins and a great contribution of epiphytes to the diversity of pteridophytes. The largest (1441 spe-

cies), mostly (ca. 87%) epiphytic family is Polypodiaceae, but with mostly terrestrial genera *Colysis* and *Leptochilus* (Zotz 2013a, who recorded that *Lepisorus* also comprises five epiphytic and 88 non-epiphytic species). Smaller such families or groups are Davalliaceae, elaphoglossoids (Dryopteridaceae) and vittarioids (Pteridaceae) (Kress 1989, Smith *et al.* 2006, Christenhusz *et al.* 2011, Zotz 2013a). A great number of epiphytic species are included in two other large families, Aspleniaceae (408 epiphytes/720 species in total) and Hymenophyllaceae (345/625) (Zotz 2013a). Psilotaceae are a small epiphytic family, and nearly a half of the species in the microphyllous Lycopodiaceae are epiphytes, while a few occur in Selaginellaceae (Zotz 2013a).

Recent molecular phylogenetic analyses have provided deep insights into the diversification and phylogeny of ferns, with results partly supporting previous classifications based on morphological and other phenetic characters and partly proposing new systems (Hasebe *et al.* 1995, Pryer *et al.* 2001, 2004, Schneider *et al.* 2004a). Most of the higher leptosporangiate ferns are suggested to have diversified in angiosperm-dominated forests, following the diversification of angiosperms in the Late Cretaceous or Paleogene (Schneider *et al.* 2004a, Schuettpelz & Pryer 2009). Fern diversification is highlighted by the evolution of epiphytes, which grow predominantly on angiospermous trees. One-third of leptosporangiate ferns are epiphytes, and epiphytic ferns account for about 10% of vascular epiphytes, a higher proportion than about 3% of all ferns within the vascular plants (Schuettpelz & Pryer 2009). There are apparently no fern epiphytes on gymnosperms (Watkins & Cardelús 2012), and epiphytic fossils of the Mesozoic in gymnosperm-dominated landscapes are very scarce compared with Cenozoic fossils (Pšenička & Opluštil 2013). If ferns have reduced water use efficiency, wetter forests may have facilitated fern diversification (Watkins & Cardelús 2012). Successful epiphytic species would have required major modification in the gametophyte generation, as well as in the sporophyte generation. Terrestrial species also radiated at this time and may

have relied on unique aspects of photobiology to take advantage of low-light terrestrial habitats (Watkins & Cardelús 2012).

The process of evolution of epiphytes from terrestrial plants, with distinct ecological shifts, remains unclear. Molecular phylogenetics has revealed the process and pattern of diversification of epiphytic ferns. Among vascular plants, ferns and lycophytes are characterized by free-living gametophytes and sporophytes, indicating that the gametophyte and sporophyte may have their own strategies for epiphytism. Comparative studies of fern gametophytes have contributed to the understanding of the evolution of epiphytism. In this paper we review recent progresses on the phylogeny of epiphytic ferns and the evolution of epiphytism in ferns, with an emphasis on Davalliaceae.

Phylogeny

Infrafamilial relationships of Davalliaceae

Molecular phylogenetic analyses show that the generally epiphytic family Davalliaceae sensu Kramer (1990a) is paraphyletic. Davalliaceae with about 50–130 species have been classified into 4–10 genera in modern classifications (Tsutsumi & Kato 2005, references cited therein). The maximum of 10 genera include *Araiostegia*, *Davallia*, *Davallodes*, *Gymnogrammitis*, *Humata*, *Leucostegia*, *Paradavallodes*, *Parasorus*, *Scyphularia*, and *Trogostolon*, recognized based on the form, dissection, and texture of leaves, scales, pubescence, and the form and size of the sori. Among the genera, the exindusiate *Gymnogrammitis* has been separated as a monotypic family Gymnogrammitidaceae, based on morphological distinction (Ching 1966), but currently, it is considered to be related to *Selliguea* in the Polypodiaceae (Schneider *et al.* 2002). Another analysis shows that four of five genera, *Araiostegia*, *Davallia*, *Humata*, and *Scyphularia*, are not monophyletic (*Parasorus* and *Trogostolon* are monotypic) (Tsutsumi & Kato 2005). *Davallodes*, together with species of *Araiostegia* and *Paradavallodes multidentata* (Hook.) Ching, forms a monophyletic clade, which is sister to the rest of

the family. *Leucostegia* was excluded from Davalliaceae (Tsutsumi & Kato 2006). Recent analyses (A. Larsson, unpubl. data, C. Tsutsumi, unpubl. data) suggest that *Davallia canariensis* (L.) Sm., the type of the genus *Davallia*, is isolated from *Davallia* although its phylogenetic position remains unclear, suggesting a more complicated phylogeny than we know and that the classification and nomenclature are not settled.

The family Polypodiaceae sens. str. is also paraphyletic. Traditional classifications had treated another epiphytic family, Grammitidaceae, as a separate family. However, molecular phylogenetic studies show that it is an ingroup of Polypodiaceae, so the emended Polypodiaceae are sometimes referred to as the polygrammoid ferns (Ranker *et al.* 2004, Schneider *et al.* 2004c).

Interfamilial relationships of Davalliaceae

Molecular phylogenetic analyses of a wide range of higher leptosporangiate ferns show that the mostly obligate epiphytic families Davalliaceae and polygrammoid ferns (Polypodiaceae + Grammitidaceae, or Polypodiaceae s.l.) form a monophyletic clade (Hasebe *et al.* 1995, Schneider *et al.* 2004a, Smith *et al.* 2006, Tsutsumi & Kato 2006), suggesting that the epiphytic life form arose in the common ancestor of these families. Thus, this epiphytic group of families forms the largest monophyletic clade, comprising ca. 1300 species and accounting for 14% of ferns. Previous data suggested that the group comprising the two families may be sister to a group of *Arthropteris beckleri* (Hook.) Mett., *Oleandra pistillaris* (Sw.) C. Chr. and *Tectaria devexa* (Kunze ex Mett.) Copel., or *O. pistillaris*, but the precise sister taxon of the families had remained uncertain due to insufficient data (Hasebe *et al.* 1995). Tsutsumi & Kato (2006) examined all of *Arthropteris*, *Oleandra* and *Tectaria*, along with other ferns, using *rbcL* and *accD* gene sequences, with result that *Oleandra* was shown to be sister to the davallioid-polygrammoid ferns (Fig. 2). The second and third sisters are a clade (Tectariaceae) of *Arthropteris*, *Quercifilix* and *Tectaria*, and a clade (Lomariopsidaceae) of *Nephrolepis* and *Lomariopsis*.

Tsutsumi & Kato (2006) showed that *Leucostegia* is sister to the calcareous-lithophytic *Hypodematum*, i.e. a member of Hypodematiaceae (Fig. 2). In previous classifications, *Leucostegia* was assigned to the Davalliaceae (e.g., Kramer 1990a). This assignment was based on similarities in morphological characters, such as the long-creeping, dorsiventral rhizome densely covered by scales and with leaves alternate on the dorsal side of the rhizome, extra-axillary lateral buds on the lateral-ventral sides, and posterior indusia. Most of the characters are shared with another epiphytic family Polypodiaceae. In contrast, *Leucostegia* differs from Davalliaceae in that the roots are scattered non-dorsiventrally around the rhizome, the stelar anatomy is simple with binary leaf traces, the scales are basifixed, and the sori are terminal and single at vein endings (Nayar & Bajpai 1976, Kato 1985).

Hypodematum has been placed in various groups, due to its specialized morphology (Iwatsuki 1964), but often is referred to the athyroid group (e.g., Iwatsuki 1964; Kramer 1990b; Hasebe *et al.* 1995). In the current classification it is separated as Hypodematiaceae (Christenhusz *et al.* 2011). *Hypodematum* and *Leucostegia* share the following characters: creeping rhizome dorsiventral and densely covered by basifixed scales and sori covered by basifixed indusia (but fixed at the base and sides in *L. pallida* (Mett.) Copel.). The simple dictyostelic vascular organization of the rhizome with binary leaf traces also accords with that of *Leucostegia* (Iwatsuki 1964, Kato & Mitsuta 1980). With the dorsiventral rhizome covered by dense persistent scales, *Hypodematum* is a lithophyte preferring limestone rocks. *Leucostegia* is also usually lithophytic or epiphytic. In conclusion, *Leucostegia*, like *Gymnogrammitis*, is excluded from Davalliaceae.

Evolution of epiphytes

Definition of life forms

Field observations revealed that Davalliaceae and related ferns have four life forms, i.e., terrestrial, climbing, secondary hemi-epiphytic, and

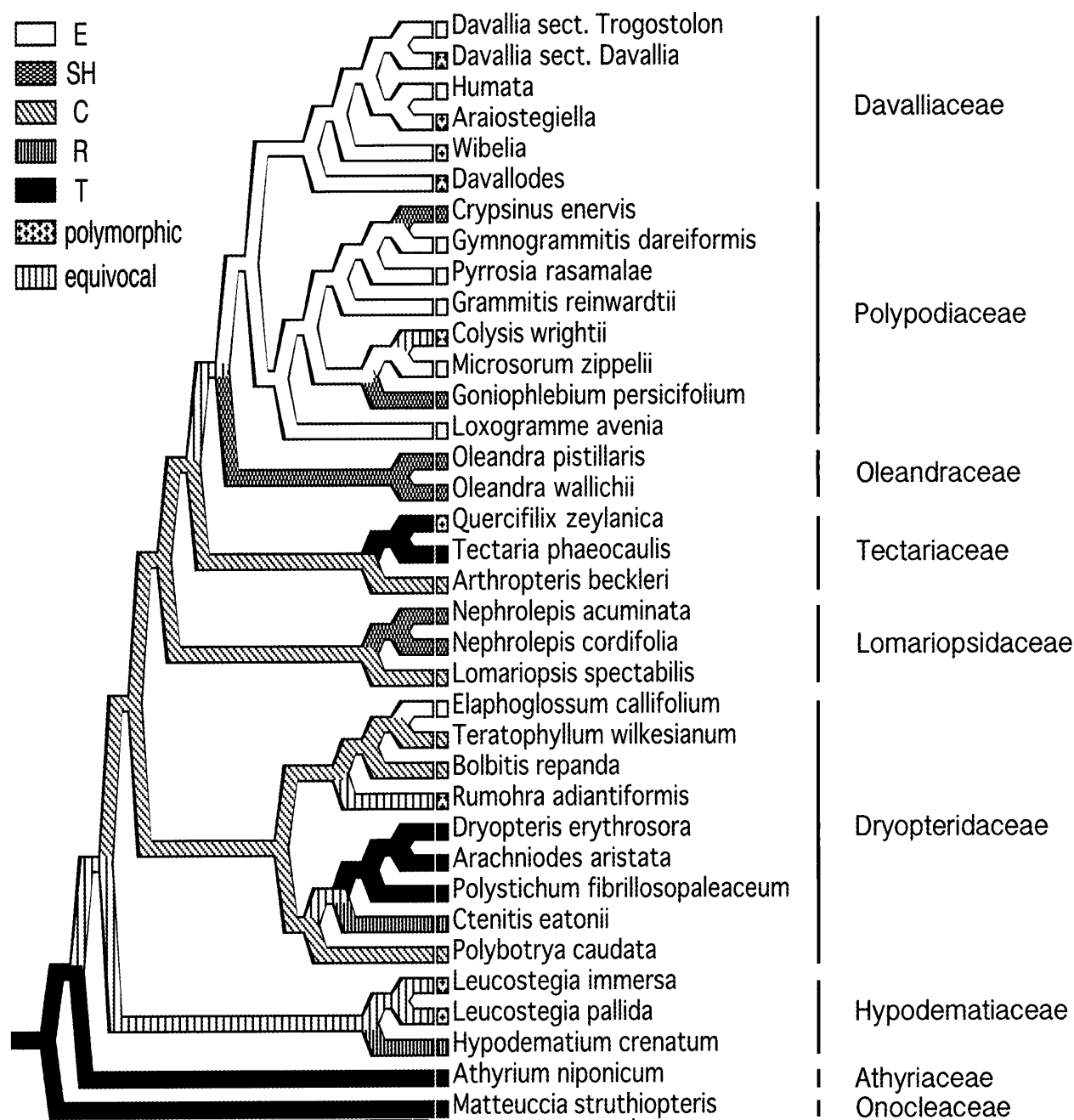


FIG. 2. Evolution of life form in Davalliaceae and related ferns inferred from ML phylogenetic tree (modified after Tsutsumi & Kato 2006). Athyriaceae and Onocleaceae are illustrated to be basal and subbasal to the rest, respectively, but form a monophyletic clade in recent phylogenetics (e.g., Rothfels *et al.* 2012). Genera and sections of Davalliaceae follow Kato & Tsutsumi (2008), and the concepts of the families on the right side follow Smith *et al.* (2006) and Christenhusz *et al.* (2011). C, climber; E, obligate epiphyte; SH, secondary hemi-epiphyte; R, lithophyte; T, terrestrial.

obligate epiphytic (Tsutsumi & Kato 2006), in accordance with the general classification for vascular plants by Benzing (1989, 1990). The life forms are theoretically characterized by the place of spore germination and the growth of gametophytes and young sporophytes, and the place of water and nutrition absorption in the following

sporophytic stage. Spore germination and the subsequent growth of gametophytes and young sporophytes, however, are often difficult to observe in the field.

Terrestrial ferns germinate, grow to maturity, and reproduce on the ground. By contrast, obligate epiphytes (e.g., *Davallia*) live on trees with-



FIG. 3. Ferns of two life forms. A. Epiphytic *Davallia denticulata* (Burm.) Mett. (Davalliaceae) on planted tree together with climbing aroid *Epipremnum aureum* (Linden ex André) G. S. Bunting (Java, Indonesia). B. Climbing *Arthropteris beckeri* (Tectariaceae) (Queensland, Australia).

out contact with soil throughout their life history beginning with spore germination on trees. They use water and nutrients exclusively available on trees (Fig. 3A). Climbers and hemi-epiphytes grow in amphihabitats. Climbing ferns (e.g., *Arthropteris*) are terrestrial during early stages of their life history when their spores germinate and the gametophytes develop into sporophytes, and then climb tree trunks (Fig. 3B). The roots are usually dimorphic; i.e., long, branched roots anchor the plants to the soil, while short epiphytic roots are borne on climbing rhizomes. If the rhizome of climbers is cut at certain heights, the distal portion above the separation becomes dehydrated, indicating that such plants cannot live without absorbing water from the ground. The underground roots absorb water and nutrients predominantly indicating that the lower portion of the rhizome with long, branched roots plays a logistic role throughout the life of the individual,

while the short epiphytic roots adhering to trees may not contribute much to water absorption. Secondary hemi-epiphytic ferns (e.g., *Oleandra*, *Nephrolepis*) are similar to climbers in their early life history, but even after the rhizomes and roots are interrupted, the ferns can live separate from the soil, like obligate epiphytes. The roots are usually monomorphic; the epiphytic roots not only adhere to trees but also absorb water and nutrients from the tree surface or from the humus that accumulates on them. In the field one may actually encounter difficulties in precisely identifying the life forms of ferns, because it is difficult to observe both young and mature plants of single species. For example, some Polypodiaceae (e.g., *Microsorium buergerianum* Ching, *M. nigrescens* (Blume) Copel., *Goniophlebium persicifolium* Bedd.) in fact are able to grow as secondary hemi-epiphytes (M. Kato, unpublished observations), though they are generally classified as epi-



FIG. 4. Secondary hemi-epiphytic *Goniophlebium persicifolium* (Polypodiaceae) (Java, Indonesia). A. Young plants wandering on the ground. B. Older plants climbing nearby tree.

phytes (Kress 1989) (Fig. 4). Thus, climbers and secondary hemi-epiphytes begin as terrestrial organisms in the early stages of their existence, starting with spore germination, and later become epiphytic.

Evolution of life form

From the character evolution of life forms based on molecular phylogenetic trees of Davalliaceae and related ferns, obligate epiphytes are hypothesized to have evolved from secondary hemi-epiphytes, or less likely from climbers (Fig. 5). Tsutsumi & Kato (2006) proposed a scenario for the evolution of the characters that define the life forms of ferns. The scenario is the most parsimonious, based on the results of ML and MP analyses of life form evolution (Fig. 2) and field observations. Evolution starts with the terrestrial life form, changes to climbing, then to secondarily hemi-epiphytic, and eventually to obligate epiphytic. It is because secondary hemi-epiphytes grow as climber in the early stage of their life history, as well as because of the presumed character evolution. The scenario comprises three successive steps that characterize the major phases of life history. The first change from terrestrial to climber involved rhizome elongation

with upward growth to allow plants to climb and the development of adhesive roots adhering to upright tree trunks. Those roots may absorb water, but much less efficiently than underground roots. Radial rhizomes changed to dorsiventral rhizomes. The next change from climber to secondary hemi-epiphyte acquired an ability to utilize water and nutrients available on the surface of trees via epiphytic roots, even under conditions in which the plants are unable to use those resources from the soil. All terrestrial plants, climbers and secondary hemi-epiphytes grow terrestrially throughout, or during the early stages of, their life cycle. Spores germinate on or below the ground and the gametophytes and then the young sporophytes grow terrestrially. The last change from secondary hemi-epiphyte to obligate epiphyte involved a shift in the place of spore germination from the ground to trees.

Epiphytes are considered to have evolved in several other pteridophyte lineages. Pathways to epiphytism may or may not be the same as the pathway in the davallioid-polygrammoid ferns discussed above. A similar pathway is likely in Elaphoglossoideae (with 600–800 species) of Dryopteridaceae, in which epiphytic *Elaphoglossum* was derived from climbers or lithophytes/

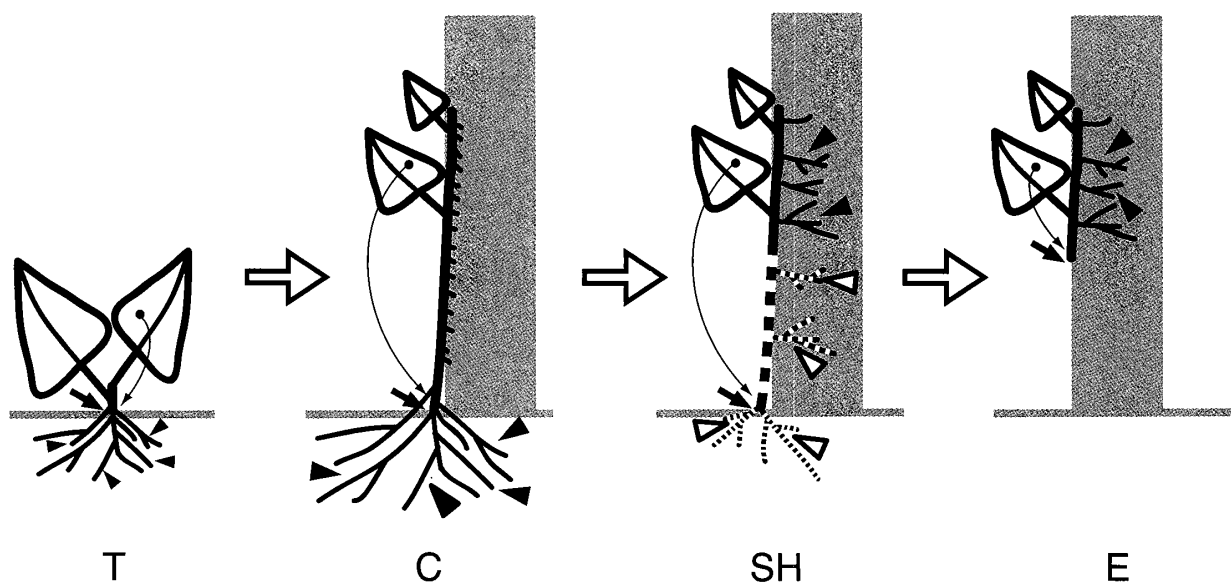


FIG. 5. Scenario of life-form evolution in Davalliaceae and Polypodiaceae, as indicated by open arrows (modified after Tsutsumi & Kato 2006). Terrestrial plant (T) and epiphyte (E) live terrestrial and on tree throughout life, respectively. Climber (C) has subterranean rhizome necessary to its life, and climbing stem attached by adhering roots. Secondary hemi-epiphyte (SH) is able to live even when aerial part is separated from terrestrial rhizome. Evolution of climber from terrestrial life form involves elongation and climbing of stem. Evolution of secondary hemi-epiphyte involves independent growth of epiphytic part of plant when separated from terrestrial part. Evolution of epiphyte involves shift of place of spore germination to tree. Solid arrows, solid arrowheads, and broken lines indicate, respectively, place of spore germination, absorbing roots (open arrowheads indicate withered roots), and withered stem and roots. Curves indicate spore dispersal.

secondary hemi-epiphytes (*Teratophyllum* and *Bolbitis*) (Tsutsumi & Kato 2006), although other genera remain unexamined. Lagomarsino *et al.* (2012) hypothesized that epiphytism in *Elaphoglossum* is derived from the ancestral terrestrial life form seen in *Bolbitis* via secondary hemi-epiphytism and then primary hemi-epiphytism in *E. amygdalifolium* (Mett.) Christ.

In vittarioids in Pteridaceae (Smith *et al.* 2006), or Vittariaceae sensu Kramer, almost all species are obligate epiphytes with short or long rhizomes (Kramer 1990c). The group is embedded within *Adiantum* (Schuettpelz & Pryer 2007), which includes terrestrial, lithophytic and rarely epiphytic species (Tryon *et al.* 1990). The epiphytic vittarioids possibly evolved directly from terrestrials or lithophytes, not *via* climbers/secondary hemi-epiphytes. The typically lithophytic *Polypodium appalachianum* Haufler & Windham (Polypodiaceae) grows as an accidental epiphyte in the microhabitat of the surface of horizontal tree branches that mimic forest floor habitats (Keller *et al.* 2003). This situation may be

similar to the initial stage in the evolution from a lithophytic lifestyle.

Hymenophyllaceae, or filmy ferns (with more than 600 species), primitive leptosporangiate ferns, are diverse in life form. They are divided into the hymenophylloides and the trichomanoids (in which several genera and subgenera are recognized). In the trichomanoids, epiphytes were inferred to have evolved from terrestrials, while hemi-epiphytes may have been derived from epiphytes or terrestrials (Hennequin *et al.* 2008, Dubuisson *et al.* 2009). The obligate epiphytes are suggested to have evolved recurrently from secondary hemi-epiphytes, and secondary terrestri- alization also took place multiple times. All obligate epiphytes, secondary hemi-epiphytes, and climbers in the trichomanoids, like those of Davalliaceae, share long-creeping rhizomes, but it is uncertain whether long-creeping rhizomes are primitive or derived. The rootless epiphytic species of *Crepidomanes* and *Didymoglossum* with root-like stems are considered to be derived (Schneider 2000). Hennequin *et al.* (2008) and Du-



FIG. 6. Epiphytic *Asplenium nidus* (Aspleniaceae) on tree trunks, with baskets formed by fascicled leaves on short rhizome (Java, Indonesia). Inset shows basket gathering plant debris, which are used as nutrient source by *A. nidus* with penetrating roots in the basket.

buisson *et al.* (2009) hypothesized that hemi-epiphytic species were derived twice from epiphytic species. The evolution of life forms in Hymenophyllaceae is complicated and accomplished with different strategies from those of the davallioid-polypodioid lineage.

In the hemi-epiphytic *Vandenboschia collariata* (Bosch) Ebihara & K. Iwats. (Hymenophyllaceae), like *Lomariopsis vestita* E. Fourn. and *L. japurensis* (C. Martius) J. Sm. (Lomariopsidaceae), the sporophytes initiate growth on the base of trees (above the ground), producing descending roots from short stems and then climbing stems to reach higher elevations (Nitta & Epps 2009, Watkins *et al.* 2010). This growth is not secondarily hemi-epiphytic, but is primarily hemi-epiphytic in Benzing's (1990) sense as in *Elaphoglossum amygdalifolium* (Lagomarsino *et al.* 2012). These primary hemi-epiphytic ferns move

from low trunks (as low-trunk epiphytes) to upper trunks (as epiphytes) during ontogeny. Close observations are necessary to identify the life forms of other ferns precisely.

The family Aspleniaceae is classified into two (less likely more) genera, *Asplenium* and *Hymenasplenium*. *Asplenium*, with a majority of species, has a number of epiphytic, lithophytic and terrestrial species but a few hemi-epiphytes, and the rhizomes of many epiphytic species are short with nest leaves (Fig. 6) (Iwatsuki *et al.* 1995, Smith *et al.* 2006). *Hymenasplenium* is primarily epiphytic or epilithic with creeping dorsiventral rhizomes. Therefore, those epiphytes may not appear to have evolved from hemi-epiphytes. A phylogenetic study showed that the most basal clades of asplenoid ferns are epiphytes (Schneider *et al.* 2004b) and so epiphytism in asplenoids may have already occurred before or at the

divergence of the group.

Lycophytes are the earliest diverged lineage of vascular plants, earlier than the diversification of ferns and seed plants and isolated from them (Qiu *et al.* 2006, Smith *et al.* 2006). The genus *Huperzia* comprises epiphytic and terrestrial species. Wikström *et al.*'s (1999) phylogenetic tree shows that epiphytism evolved once from the terrestrial *H. selago* (L.) Bernh. ex Schrank & Mart. group. Most modern epiphytic lycophyte species are suggested to have diversified in the late Cretaceous in tropical forests dominated by angiosperms rather than gymnosperms or ferns (Wikström *et al.* 1999, Schuettpeltz & Pryer 2009). The pattern of diversification of epiphytic lycophytes in response to the changes in forest vegetation is quite similar to that in epiphytic ferns, even though the two are deeply diverged lineages of vascular plants. Because there is no hemi-epiphytic species of *Huperzia*, the epiphytes possibly evolved directly from terrestrials, as in the vittarioids (see above), but it is an open question. Wikström *et al.* (1999) also stressed that terrestrialization of epiphytic *Huperzia* occurred at least twice about 15 million years ago (Mid Miocene) and was triggered by the development of open, alpine vegetation resulting from mountain building during the much later Andean orogeny.

In contrast to the homosporous Lycopodiaceae, there are no epiphytes in the heterosporous, microphyllous Isoetaceae, and there are only several epiphytic/lithophytic species in Selaginellaceae. *Isoetes* is aquatic and, although most species of *Selaginella* are terrestrial, its ancestor may have been aquatic (Kato 2005). A paleobotanical report indicates the occurrence of *Selaginella*-like epiphytes from the Pennsylvanian (Pšenička & Opluštil 2013). There are also no heterosporous epiphytes in ferns, which are mostly homosporous and all of a small number of heterosporous species (e.g., *Marsilea*) are aquatic. Obligate intergametophytic cross-fertilization in small endosporic gametophytes, characteristic of heterosporous plants, may be difficult in trees, where water is prone to be deficient between gametophytes. However, it is reported that most ho-

mosporous fern epiphytes are also outcrossers (Ranker 1992, Hooper & Haufler 1997, Chiou *et al.* 1998), although it may be assumed that tree canopy releases inbreeding pressures and facilitates more rapid speciation of epiphytes (Watkins & Cardelús 2012). In the seed plants, which are also heterosporous, fertilization occurs regularly within ovules (in gymnosperms) and carpels (in angiosperms) with inner archegonia, which avoid primitive fertilization requiring external water. Thus, epiphytism with water limitation might have evolved in an opposite direction to heterospory, which might have happened in aquatic environments (Kato 2005). In general, epiphytism in heterosporous plants perhaps evolved in angiosperms (only several species in extant gymnosperms) after the appearance of the seed habit, along with the herbaceous or shrubby habit. It is most likely that the radiation of epiphytic angiosperms followed the appearance of modern forest vegetation dominated by woody angiosperms in the Late Cretaceous and Paleogene.

Salient traits correlated to life form

There are high correlations between the life forms and morphological traits. The rhizomes are long-creeping in all climbers, all secondary hemi-epiphytes, and many obligate epiphytes. In comparison, in terrestrial species the rhizomes range widely from short or tall and erect to long-creeping. The correlation of life form and rhizome habit, along with phylogenetic relationships, support Dubuisson *et al.*'s (2003) hypothesis that long-creeping stems allow climbers and secondary hemi-epiphytes to colonize vertical supports rapidly. In an extreme case, the rhizome of the secondary hemi-epiphytic *Oleandra pistillaris* has remarkably long (to 2 m) internodes (Tsutsumi & Kato 2010). By contrast, small obligate-epiphytic grammitids (e.g., *Grammitis reinwardtii* Blume examined) and some polypods (e.g., *Lepisorus*) have probably derived short rhizomes, a possible product of weak selective pressure on rhizome length in epiphytes. It is possible that vittarioid ferns have primarily short rhizomes.

The rhizomes of plants growing on trees or rocks may be dorsiventral in relation to the surface of the substrata. Dorsiventrality of fern rhizomes is indicated by the arrangement of lateral organs produced on the rhizomes; the roots, which are least resistant to drought, are inserted on the ventral surface and penetrate the soil or bryophyte layer, while the leaves are dorsal or dorso-lateral. Dorsiventral rhizomes tightly attached to trees by such roots are seen in all of climbers, secondary hemi-epiphytes and obligate epiphytes (Tsutsumi & Kato 2006). For example, the rhizome is dorsiventral in the climbing *Stenochlaena* (Blechnaceae) and *Arthropteris* (Tectariaceae) and the hemi-epiphytic or epiphytic Davalliaceae and Polypodiaceae. But the non-creeping rhizome of Polypodiaceae, e.g., *Oleandropsis*, grammitids, are not dorsiventral (Kato & Darnaedi 1996).

Scales, major dermal appendages of rhizomes and leaves, are basifixed with a broad base, or stalked with a peltate or pseudopeltate shield parallel to the rhizome surface. In terrestrial ferns the scales cover rhizome apices and leaf primordia, and are deciduous or nearly so on the older portions, protecting these fragile organs from desiccation and injury. Stalked scales are seen in several groups of ferns, e.g., Davalliaceae, some Dryopteridaceae, some Lomariopsidaceae, Nephrolepidaceae, Oleandraceae, most Polypodiaceae (Kramer & Green 1990), and *Saccoloma* (Saccolomataceae) (Nair 1979). All of them but the last are epiphytic in a broad sense (Kramer & Green 1990). Phylogenetically, the climbing *Arthropteris*, along with *Quercifilix* and *Tectaria*, and then the secondary hemi-epiphytic *Oleandra* diverged before the diversification of mostly obligate-epiphytic Davalliaceae and Polypodiaceae (Tsutsumi & Kato 2006). The scales of most Davalliaceae have stalks deeply sunken in rhizome holes, while those of the low-trunk epiphyte, *Davallodes hymenophylloides* (Blume) M. Kato & Tsutsumi, and the secondarily hemi-epiphytic *Oleandra* have short stalks sunken in shallow depressions of the rhizome and central shield cells with dense contents. The scales of the climbing species of *Arthropteris* and secondarily hemi-ep-

iphytic *Nephropteris* have short stalks attached to the even surface of the rhizome (Tsutsumi & Kato 2008). This close phylogenetic linkage of the scales and life forms in Davalliaceae and related ferns suggests a possibility that the roles of the elongate stalked scales are significant for an epiphytic lifestyle (Tsutsumi & Kato 2008). The role of the scales of Davalliaceae may be multiple. The persistent, tightly appressed, multi-layered scales, with stalks inserted in narrow holes on the rhizome and horizontal shields, are likely to protect the rhizome from desiccation, which is prone to happen to epiphytes, and to store water externally (Fig. 7). A microautoradiographical analysis suggested that the peltate trichomes of the epiphytic Tillandsioideae (monocots, Bromeliaceae), which are borne on the surface of leaves, absorb water and nutrients (Benzing *et al.* 1976, Benzing 2000). Other epiphytes also have similar stalked dermal appendages, e.g., the stellate hairs in *Pyrrosia* (Polypodiaceae) and the capitate trichomes with the lateral walls of the stalk cutinized in Pleurothallidinae (Orchidaceae), which were suggested to have the ability to absorb water (Müller *et al.* 1981, Pridgeon 1981). A similar capability of absorbance may be possible in the scales of Davalliaceae.

Other characters dominant in epiphytes include leaf abscission, thick and firm leaves, and crassulacean acid metabolism (CAM), all being adaptations to drought (Zotz & Hietz 2001). In Davalliaceae and Polypodiaceae, like in other ferns, the leaves are deciduous with abscission layers at the base of the leaves or pinnae. Leaves are firmly chartaceous to coriaceous with a thick cuticular layer, but are sometimes herbaceous. CAM epiphytes absorb carbon dioxide while the stomata are open during the night and assimilate while the stomata are closed during the day; stomatal closure reduces transpiration. The CAM pathway occurs in several fern families (Holtum & Winter 1999, Martin *et al.* 2005). The nitrogen cycle of epiphytic ferns in tropical rainforests functions independent of that in terrestrial ferns (Watkins *et al.* 2007c).

Organismal association is prominent in epiphytic ant-plants of *Microgramma* subgenus *So-*

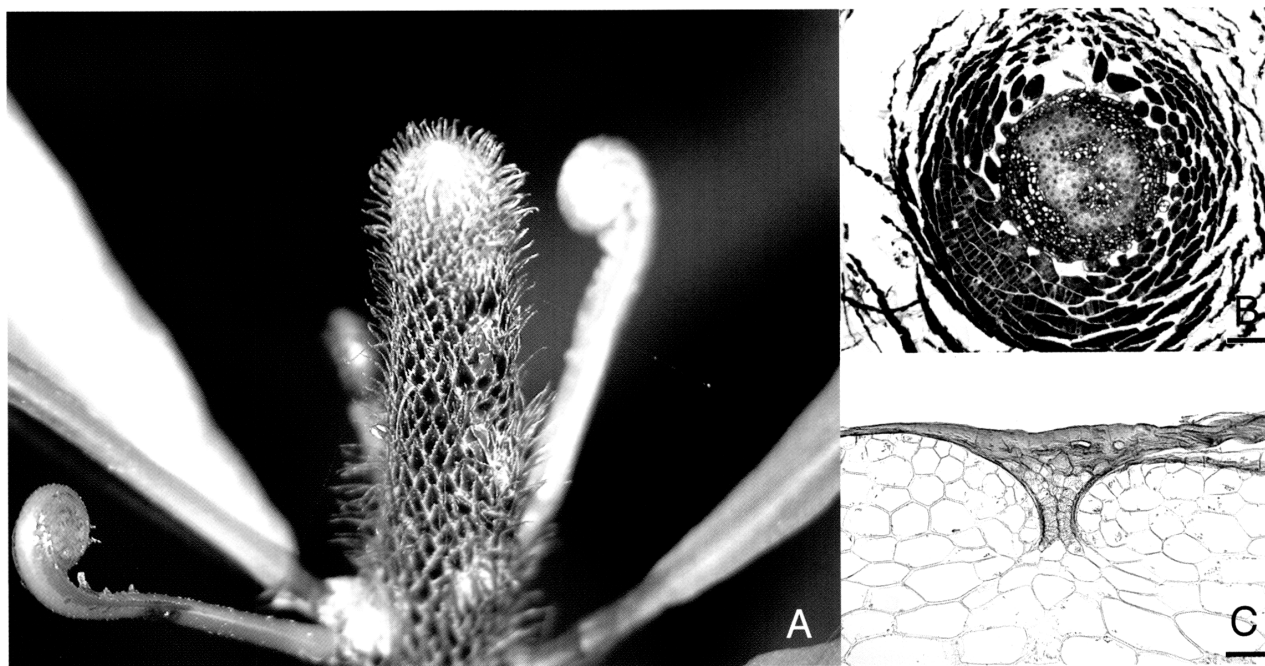


FIG. 7. Scales on fern rhizomes. A. Imbricate scales on stem tip in secondary hemi-epiphytic *Oleandra pistillaris* (Oleandraceae) (Java, Indonesia). B. Cross section of stem tip with multilayered scales in epiphytic *Davallia trichomanoides* Blume (Davalliaceae). C. Longitudinal section of peltate scale with stalk inserted into rhizome hole in *Davallia trichomanoides*. Adjacent scale is close to stalk of scale. Scale bars = 70 μ m.

lanopteris and *Lecanopteris* (Polypodiaceae), which receive nutrients from ants and, in turn, provide ants with nesting spaces within the hollow rhizomes (Fig. 1) (Gómez 1974, Gay 1993). Vittarioid *Antrophyum lanceolatum* (L.) Kaulf. has no special spaces, but forms rhizome mats surrounded by ant debris (Watkins *et al.* 2008).

Symbiotic associations with fungi are weak in epiphytic ferns in comparison with terricolous ferns (Wang & Qiu 2006). Hawaiian epiphytic species have a lower frequency (55%) of mycorrhizal colonization than terricolous species (83%), and epiphytic Polypodiaceae (including grammitids), Hymenophyllaceae and *Elaphoglossum* (Dryopteridaceae) have lower frequencies than terricolous ferns (Gemma *et al.* 1992).

Pteridophytes, or ferns and lycophytes, are characterized by two independent generations, gametophytic and sporophytic. In contrast, other land plants have heterotrophic generations: the sporophytes of bryophytes depend on their gametophytes, while seed plants have megagametophytes embedded in sporophytes. The gametophyte of pteridophytes has a varied, ill-differentiated morphology ranging from membranous

heart-shaped to ribbon-like, filamentous and to cylindrical and massive, while the sporophyte comprises differentiated organs, stem, leaf, and root (but rarely is rootless). The gametophyte grows from a germinating spore in the early stage of the life cycle. In all terrestrial, climbing and hemi-epiphytic species, the gametophyte is terrestrial (including subterranean), and the gametophytes of most terrestrial leptosporangiate ferns are simple, heart-shaped with one meristem in the notch, although they may elongate before fertilization. In epiphytes, the gametophyte is also epiphytic, and it should be stressed that the epiphytic gametophytes of Hymenophyllaceae, vittarioids (Pteridaceae), elaphoglossoids (Dryopteridaceae), and grammitids (Polypodiaceae) are complex, strap-shaped, ribbon-like or filamentous, branched with multiple meristems, often gemmiferous (to reproduce clonal gametophytes), and long-lived (Stokey & Atkinson 1958, Atkinson & Stokey 1964, Nayar & Kaur 1971, Yoroi 1972, Dassler & Farrar 1997, 2001, Farrar *et al.* 2008, references cited therein). However, the epiphytic gametophytes of Davalliaceae, Polypodiaceae (which are strap-shaped in some species),

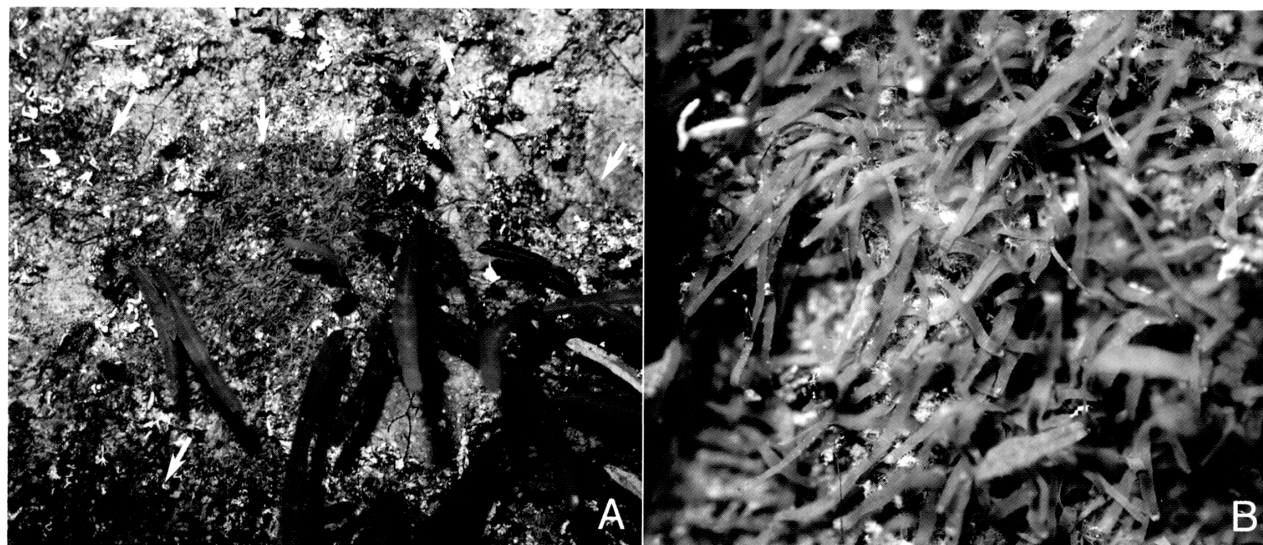


FIG. 8. Lithophytic *Phanerosorus major* (Matoniaceae) on calcareous rock cliff (Seram, Indonesia). A. Gametophyte populations (indicated by arrows) co-occurring with young sporophytes (with linear-oblong leaves), which may result from polycarpy. B. Magnification of thicket of ribbon-like branched gametophytes.

and *Oleandra*, which is sister to the clade of the two families, are usually heart-shaped with a meristem in the notch, as in terrestrial gametophytes, while they are ribbon-like or strap-like in some microsoroids and grammitids of Polypodiaceae (Stokey & Atkinson 1958, Momose 1967, 1968, Nayar *et al.* 1968, Nayar & Kaur 1971, Atkinson 1973, Watkins *et al.* 2011). Also, the gametophytes of the epiphytic *Asplenium nidus* and allies (Aspleniaceae) are heart-shaped (Momose 1967, 1968) and short-lived (i.e., mature sexually within a few months in culture) (Yatabe *et al.* 2001, K. Yamada, personal communication). The responses of gametophytes to their environment are therefore not simple. The strap-shaped, ribbon-like and filamentous epiphytic gametophytes are argued to be long-lived and have a lower rate of sporophyte production in the relatively stable environment of mossy trees, in contrast to short-lived gametophytes growing in the frequently disturbed terrestrial environment (Farrar 1990, Chiou & Farrar 1997, Chiou *et al.* 1998, Watkins *et al.* 2007a). The epilithic gametophytes of *Phanerosorus major* Diels (Matoniaceae), a primitive fern, are also long ribbon-like and long-lived and grow together with their sporophytes on dry vertical limestone cliffs, while the terrestrial gametophytes of the related *Matonia* are elongate and heart-shaped (Fig. 8) (Yoroi & Kato 1987).

Watkins *et al.* (2007a, b) argue that in desiccation-prone, rarely disturbed canopies, epiphytes have a complex morphology of gametophytes exhibiting water-holding capacity or desiccation tolerance, and longevity, waiting for favorable conditions to produce sporophytes through outcrossing. However, this relationship of gametophyte eco-morphology and life form should be tested using a wider array of species. The gametophytes of the epiphytic families Davalliaceae and Polypodiaceae differ little from terrestrial gametophytes, like the epiphytic gametophytes of the *Asplenium nidus* group. In contrast to other Polypodiaceae, the gametophytes have a prolonged life span in grammitids with high species richness (~750 species) and chlorophyllous (non-dormant?) spores. Schneider *et al.* (2004c) argued that all or part of these features of grammitids may be correlated with the remarkably higher rate of nucleotide substitution in those ferns than in other polypods. In the primary hemi-epiphytic *Elaphoglossum*, the gametophytes are strap-shaped and long-lived (Chiou *et al.* 1998). The findings indicate that there are different strategies in gametophyte evolution in different evolutionary lines of ferns. In the generation phase and simple morphology, fern gametophytes are comparable to bryophytes (gametophyte generation), which are descendants of the earliest land

plants. The bryophytes exhibit vegetative desiccation tolerance, which involves constitutive cellular protection mechanisms (Oliver *et al.* 2005). Rapid recovery from dehydration (poikilohydry), which is rather common in bryophytes, is also known in the gametophytes of some pteridophytes. Farrar *et al.* (2008) stress the significance of the gametophyte generation in the ecology and evolution of epiphytic ferns and lycophytes.

Perspectives

Life form—The most fundamental issue to be clarified is to precisely identify the life forms of ferns in nature. It is usually difficult to gain information from herbarium specimens, because many specimens are fragmentary and growth data are often insufficient. It may also not be easy to perform long-term field observations to identify differences between climbers and secondary hemi-epiphytes, the difference between primary hemi-epiphytes and secondary hemi-epiphytes, and the difference between hemi-epiphytes and holo-epiphytes. Zotz (2013b) proposes abandoning the term ‘secondary hemi-epiphyte,’ which is ambiguous to him, and to use ‘nomadic vine’. Precise identification of the life form of any species in the field is a requisite for investigating the evolution of epiphytism. Furthermore, the ecological boundary of the tree base and ground is often obscure because coverage by bryophytes often provides similar habitats.

Spore and gametophyte—Ferns with free-living gametophyte and sporophyte generations provide a special opportunity to investigate the evolution of epiphytism. The spore is the initial stage of ontogeny and germinates when imbibed by external water, e.g., stored water, rainfall. Water is more readily available on the humid ground and the base of trees in shade than on exposed ground and on upper tree trunks and branches. Therefore, the spores of terrestrial ferns are able to germinate more successfully on the humid ground. Moreover, the response of spore germination to water may differ with life form. It would be interesting to know whether the spores of epiphytic

ferns are able to germinate at lower water level than those of terrestrial ferns. If not, epiphytes will be able to survive more rigorously in more xeric habitats during later stages of ontogeny.

Ecological (e.g., growth longevity, desiccation tolerance) and reproductive characterization (e.g., asexual propagation, breeding system, monocarpic or polycarpic sporophyte production) of gametophytes is necessary to understand the general aspect of gametophytes of different life forms. The gametophytes are still terrestrial in climbers and secondary hemi-epiphytes, possibly partly because terrestrial gametophytes are more sensitive to desiccation, which often happens on trees, and because external water necessary for fertilization is more available on the ground. The hypothesis of the delayed evolution of epiphytic gametophytes should be tested by comprehensive comparative analysis of terrestrial gametophytes of terrestrial, climbing and secondary hemi-epiphytic species and epiphytic gametophytes of holo-epiphytic species as well as primary hemi-epiphytes. The gametophytes may have different characteristics in epiphytes derived through the hypothesized delayed or simultaneous evolution. Comparison of their gametophytes may make the different pathways clearer. The most conspicuous change in the gametophyte generation includes the establishment of gametophytes on trees, which are prone to drying and are stable. Epiphytic ferns are often associated with epiphytic bryophytes. McCarthy (2007) showed that in co-cultures with epiphytic bryophytes, the bryophytes have a negative impact on the gametophyte development of terrestrial ferns, perhaps through allelopathy, compared with that of epiphytic ferns, and this interaction appears to represent a limiting factor for terrestrial ferns in epiphytic communities. Further comparative eco-physiological studies of fern gametophytes are necessary for better understanding the evolution of epiphytism.

Epiphytism and terrestrialization—Ecological shifts are bidirectional, from terrestrial to epiphytic and from epiphytic to terrestrial in, e.g., Hymenophyllaceae and possibly Aspleniaceae. Epiphytism is gained by stepwise or abrupt evo-



FIG. 9. Epiphytic *Pyrrosia piloselloides* (Polypodiaceae) on tree branches of *Crescentia cujete* L. (Bignoniaceae) (Java, Indonesia). Branches infested by epiphytes (on right) are leafless and eventually wither, while those without epiphytes (on left) are leafy and healthy. Inset shows roots from creeping stems adhering to branch.

lution, but the process of terrestrialization is less certain. The dynamic processes of ecological shifts will be revealed by phylogenetic, ecological and evolutionary studies.

Interactions between epiphyte and host plant—Epiphytes typically use trees as substrata, on which they live, and epiphytism is often mediated by epiphytic bryophytes. There may be interactions among them. Water-holding capacity of microhabitats provided by the usually rough host-trunk bark or epiphytic bryophytes is the most important and limiting factor for epiphytes growing in water-deficient habitats. Epiphyte transplant experiments with *Polypodium polypodioides* (L.) Watt [= *Pleopeltis polypodioides* (L.) E. G. Andrews & Windham] show that the transplanted fern prefers host trees with high water-holding capacity, on which it grows in nature

(Callaway *et al.* 2002). Tree-fern trunks with root mantles can provide favorable habitats for particular fern epiphytes called “tree-fern specialists” (Moran *et al.* 2003). The “specialists” include species of a wide systematic range of genera, *Asplenium*, *Blechnum*, *Campyloneuron*, *Dryopteris*, *Hymenophyllum*, *Nephrolepis*, and *Trichomanes*. In addition, species of *Abrodictyum*, *Costaricia*, *Terpsichore*, and *Tmesipteris* are described to grow on tree-fern trunks in local floras (e.g., Brownlie 1969, Iwatsuki *et al.* 1995, Moran & Riba 1995, McCarthy 1998, Brownsey & Smith-Dodsworth 1989). Moran *et al.* (2003) also suggest that the tree-fern root mantle has a chemical substance to inhibit algae and fungi, competitors to the ferns, but interactions via chemical substances are poorly known. The characteristics and degree of interaction should be clarified

to better understand the ecology and evolution of epiphytism.

Mildly hemiparasitic epiphyte—Is the holo-epiphyte at the end of the evolution of life forms? There are epiphytic parasites utilizing water and nutrition from trees in angiosperms (typically mistletoes), but neither holoparasite nor hemiparasite is so far known in epiphytic ferns (Poulin *et al.* 2000). *Pyrrosia piloselloides* (L.) M. G. Price (Polypodiaceae) is an epiphyte usually growing on twigs of trees (twig epiphyte), and comprises a desiccation-tolerant CAM sporophyte and non-CAM gametophyte (Ong *et al.* 1986, Ong & Ng 1998). The gametophyte is heart-shaped and drought-tolerant with propagation ability. Field and experimental observations suggest that it is a mild hemiparasite (Ruinen 1953). Twigs infested by the fern are apt to dry, while infested thick branches and trunks are not apparently affected (Fig. 9). If its life form is such, it can be hypothesized that epiphytes may evolve further to a mildly hemiparasitic lifestyle, and possibly at least part of epiphytic ferns are mild hemiparasites. This mild hemiparasitism is termed epiphytosis (Ruinen 1953). Epiphytosis is known in several angiosperm families and ferns (Went 1940, Ruinen 1953, Johansson 1974). Those epiphytes have root hairs penetrating into host plants and are mycorrhizal (Ruinen 1953, Furman 1959, Johansson 1974). Mild hemiparasitism of epiphytes will be a target of phylogenetic, morphological, eco-physiological analysis of life-form evolution.

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